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THE CHROMOSOMAL LOCALIZATION OF FIVE FACTORS DETERMINING
DURATION OF LIFE IN DROSOPHILA MELANOGASTER.

DISSERTATION

Submitted to the School of Hygiene and Public Health
of the Johns Hopkins University
in conformity with the requirements for the degree of
Doctor of Science in Hygiene.

Bienvenido Maria Gonzalez y Sioco

November 1922.

THE HISTORY OF THE
CITY OF BOSTON

FROM THE
FUNDAMENTAL CHARTERS
TO THE PRESENT
BY
JOHN H. COOPER

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THE CHROMOSOMAL LOCALIZATION OF FIVE FACTORS DETERMINING DURATION
OF LIFE IN DROSOPHILA MELANOGASTER

Introduction

In the first paper of a series on the experimental study of duration of life Pearl and Parker (1) showed that there was a marked difference in the duration of life and in the form of the l_x curve in wild type stocks of Drosophila and a synthetic quintuple mutation stock. It was also pointed out in a general way that this difference was hereditary and Mendelian.

Previous to the work of Pearl and Parker (1-7) there have been a few other studies on the duration of life of Drosophila. In 1911 Moenkhaus (8) made a casual reference to the fact that female flies were kept alive 153 days. In 1913 Hyde (9) in studying fertility and sterility found two strains of Drosophila which differed greatly in their duration of life. On breeding these he found evidence of segregation of long and short lived flies in the second filial generation (F_2). Loeb and Northrop (10-12), Northrop (13), and Lutz (14) made a number of experiments on the effects of food and temperature on the duration of life of Drosophila. All this early work is adequately reviewed by Pearl and Parker (loc.cit).

From the above papers, and the facts gathered together by Pearl (15) from the general field of biology, there seems to be little room for doubt as to the hereditability of duration of life. This fact being established, the next obvious step is to study what this factor is or what the factors are that control this method of inheritance. We do know from the work of Morgan (16) and others, of numerous physical characters of an individual directly traceable to the active units of the

nucleus of a cell - the chromosomes, and we know something of the behavior of these chromosomes, and the genes that compose them, to bring about inheritance. But what bearing do the chromosomes, or the separate genes that make up the chromosomes, have on duration of life? These then are the questions for which we seek an answer, and it is the object of this paper to present certain detailed data on these points.

Materials.

The stocks used were the Old Falmouth (wild) and the synthetic stock containing five mutants obtained from Morgan's laboratory. For convenience, the description of these two stocks as given in the first paper of Pearl and Parker is herewith reproduced:

1. Old Falmouth, Wild type fly, long bred in Morgan's laboratory.
More inbred than 2 (New Falmouth)
4. Quintuple. A synthetic stock, carrying five second chromosome mutations, each in homozygous form, as follows: black, purple, vestigial, arc, and speck. Other characters wild type (Morgan). A brief description of these mutants is as follows:

Black is a color factor affecting the body and the extremities.
Purple is an eye color factor of the hue indicated by its name.
Vestigial is a wing mutation in which the flies have tiny scales in place of wings. The "balancers" (halteres) are similarly modified, though not to the same degree as the wings.
Arc is a wing mutation in which the wings are bent downward in an even curve, presenting a convex surface.
Speck has reference to a minute and intensely black spot in the axil of each wing.

A more detailed account and description of the above mutants may be found in

Bridges and Morgan (17).

The latest map of the second chromosome as given by Bridges (18) is reproduced in Fig. 1 with the characters involved in italics.

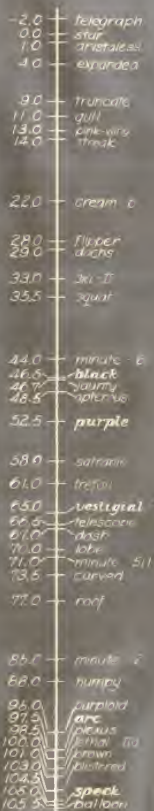


Fig. 1. Map showing the distribution of mutant loci in the second chromosome of *Drosophila melanogaster* (Oct. 15, 1920). The five mutants involved in this study are in italics.

Methods.

The technique was in general the same as that described by Pearl and Parker (1). Individual matings were made with flies half a day old or younger and placed in half-pint milk bottles provided with banana agar media. On the sixth or seventh day the parents were transferred to a second half-pint bottle. The progeny from these bottles for nine days, counting from the first day hatches were observed, were emptied into 1 - ounce vials containing banana-agar and these were kept separate and labeled as born on that day, and their duration of life observed. After nine days hatching the half-pint bottles were discarded. The parents have been transferred in the meanwhile into vials for observation of their duration of life also. The bottles were examined for dead flies every day, and they were changed three times during the week to give the flies fresh food. The method of handling the records was the same as that described in Pearl and Parker (1) and need not be repeated here. All these flies were kept at a constant temperature of 25° C in an electric incubator.

Acknowledgments.

This work was undertaken under Dr. Raymond Pearl, head of the Department of Biometry and Vital Statistics of this School, from whom I received most valuable advice and encouragement. Miss Sylvia L. Parker, associate in the Department, was a constant counsellor in the details of the experimental work. Without the help of Mr. James Krucky in the preparation of media, this work could not have proceeded with the rapidity that it has. I also wish to express my indebtedness to Misses Beryl L. Reed and Mary Connors for punching my records into cards for mechanical tabulation.

Procedure.

Reciprocal crosses of the wild and quintuple stock were made and the F_1 's mated. Cross-overs were observed and as many combinations as possible were obtained

and purified. These new combinations were labeled according to their mutant phenotypic characters as follows:

00	b	(black)
01	pr	(purple)
02	vg	(vestigial)
03	a	(arc)
04	sp	(speck)

10	bpr
11	b vg
12	b a
13	b sp
14	prvg
15	pr a
16	pr sp
17	asp

20	bpr vg
21	bpr a
22	bpr sp
23	b asp
24	pr asp
25	vg asp

30	bpr asp
31	b vgasp
32	prvgasp

The above, together with the original stocks, make a total of twenty-four different combinations.

Inasmuch as the character arc is shielded when in combination with vestigial, all vestigial stocks were tested for the presence of arc towards the end of the experiment. They were mated with a stock pure for arc and containing no other mutant, and therefore dominant for vestigial. All stocks containing arc should give 100 per cent arc progeny if they are pure for this character; vice versa, they should show 100 per cent straight wing (dominant to arc) if they are pure for the absence of the character arc. An intermediate condition shows impurity as far as the character arc or its dominant allelomorph is concerned. Three males and three females from each bottle where progeny were obtained for the duration of life experiments were thus tested. The test revealed the following:

Table I

Test of Vestigial Stocks for Arc.

Serial No.	Original Designation	Result of Test	New Designation
.02	vg	No arc	same
.11	b vg	No arc	"
.14	prvg	No arc	"
.20	bprvg	Not pure	bprvga/
.25	vgasp	Pure for arc	same
.31	b vgasp	Not pure	b vga/sp
.32	prvg asp	No arc	prvg sp
.	Quintuple bprvgasp	Pure for arc	same

Fertility.

It was the plan to raise at least five hundred individuals for each strain. To this purpose as many matings were started as were necessary to produce at least five hundred flies for the duration of life experiments. Table 2 shows the strains, the number of matings, the total progeny, and the average progeny for nine days for the fertile matings.

Table 2

Strain	No. of Fertile Matings	Progeny			Per cent Males	Average Progeny per Fertile Mating
		♂	♀	Total		
Wild	5	560	676	1236	45	247
Quintuple	18	365	420	785	46	44
b	5	335	355	690	49	138
pr	6	944	1006	1950	48	325
vg	10	245	288	533	46	53
a	7	417	470	887	47	127
sp	6	301	318	619	49	103
bpr	6	697	787	1484	47	247
b vg	5	307	388	695	44	139
b a	6	428	466	894	48	149
b sp	16	528	601	1129	47	71
prvg	10	568	523	1091	52	109
pr a	5	497	652	1149	43	230
pr sp	13	1465	1750	3215	46	247
asp	6	315	321	636	50	106
bprvg a/	9	600	616	1216	49	135
bpr a	5	413	574	987	42	197
bpr sp	27	432	624	1056	41	39
b asp	17	312	270	582	54	34
pr asp	6	331	376	707	47	118
vgasp	8	287	279	566	51	71
bpr asp	26	400	576	976	41	38
b vga/sp	16	320	306	626	51	39
prvg sp	5	276	302	578	48	116
Totals	243	11343	12944	24287		

The above table shows at a glance the wide variability in fertility of the different strains.

If a table were made up of the fertility value of each mutant, using strains containing one and two mutations* only, we would have the following:

*Strains involving more than two mutations, would tend to mask each other's effects to a degree that would render their grouping valueless.

Table 3

Fertility Value of Mutants

Strains	Total Progeny	Average
b, bpr, b vg, b a, b sp	744	149
pr, bpr, prvg, pr a, pr sp	1158	232
vg, b vg, prvg	301	100
a, b a, pr a, asp	612	153
sp, b sp, pr sp, asp	527	132

A further examination of the table discloses the fact that the strains having high fertility usually have purple, and those of low values almost invariably contain speck. No conclusion can be drawn from the above table as the number of matings involved is very small. There is the strong suggestion, however, of the presence of a gene or genes determining fertility closely linked to one or more of the mutants studied. It is hoped that at some future time a further study of this character will be made.

The Five Pure Mutants

Table 4 gives the survivorship data of the five pure mutants and the original stocks.

Table 4

Survivorship Distribution of Original Stocks and Single Mutants (Both sexes included, not weighted).

Age in Days	Number of Survivors up to Indicated Age						
	Wild	Quintuple	Black	Purple	Vestigial	Arc	Speck
1	1000	1000	1000	1000	1000	1000	1000
4	998	955	991	995	996	986	985
7	992	683	987	939	938	938	977
10	971	424	974	873	809	873	963
13	948	269	970	791	664	813	932
16	901	168	949	711	527	760	900
19	882	115	928	622	394	709	884
22	858	75	890	558	306	643	855
25	831	48	854	495	206	575	827
28	799	31	832	425	150	464	792
31	743	13	768	338	105	402	745
34	705	6	690	218	62	316	687
37	592	5	619	151	43	241	643
40	519	1	503	99	30	165	614
43	424	0	420	67	8	107	544
46	342	-	371	34	2	62	468
49	247	-	293	20	0	32	417
52	194	-	241	7	-	15	333
55	117	-	196	3	-	2	273
58	88	-	119	1	-	1	207
61	67	-	65	0	-	1	149
64	45	-	30	-	-	0	102
67	32	-	20	-	-	-	50
70	20	-	14	-	-	-	24
73	8	-	3	-	-	-	15
76	1	-	1	-	-	-	2
79	0	-	0	-	-	-	2
82	-	-	-	-	-	-	0

Abs.No.of flies	1236	785	690	1950	533	877	619
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Figure 2 shows the course taken by the lines graphically on a logarithmic scale (19). It may be observed that neither black nor speck trace a survivorship curve much different from the wild parent. Purple and arc are considerably lower than the wild stock but higher than the quintuple. The life curve of vestigial is the one closest to the quintuple, though not quite as low as this.

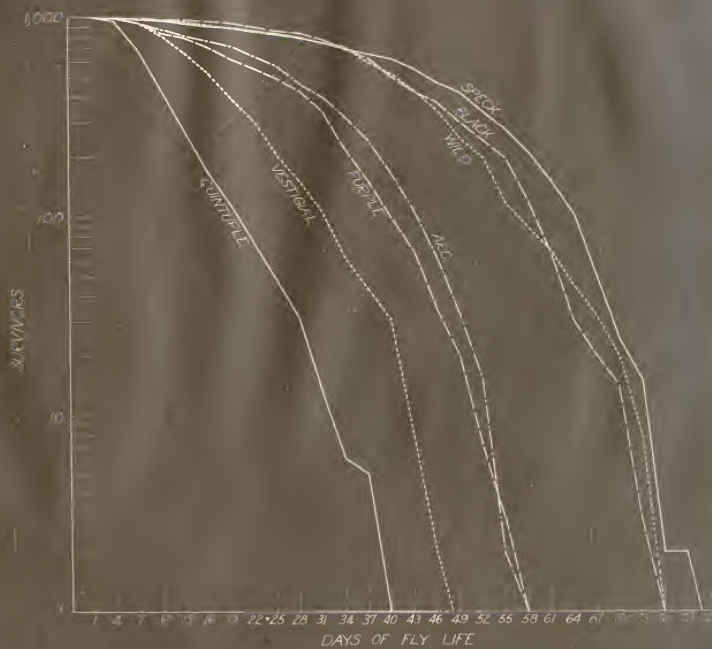


Fig. 2. Survivorship graphs of original stocks and single mutants. Both sexes.

Inasmuch as these mutations affect the duration of life of the two sexes differently, it is interesting to note just what are the differences in the various strains and how such variations are affected by the combination of two or more mutants in a single individual. The data in Table 6 are taken from Table 5.

Table 5

Duration of Life of Different Strains

Strains	Mean Duration of Life			Difference between males and females $\delta - \eta$	Difference P.E. of Diff.
	Both sexes (actual number)	Males	Females		
Wild	39.47 $\pm$.28	38.08 $\pm$.36	40.62 $\pm$.42	- 2.54 $\pm$.55	4.62
Quintuple	10.88 $\pm$.16	9.45 $\pm$.17	12.12 $\pm$.25	- 2.67 $\pm$.30	8.90
Black	40.68 $\pm$.50	41.03 $\pm$.53	40.33 $\pm$.51	+ 0.70 $\pm$.74	.95
Purple	24.54 $\pm$.18	27.42 $\pm$.27	21.83 $\pm$.23	+ 5.59 $\pm$.35	15.97
Vestigial	18.22 $\pm$.29	14.98 $\pm$.28	20.98 $\pm$.40	- 6.00 $\pm$.49	12.24
Arc	26.81 $\pm$.29	25.20 $\pm$.33	28.24 $\pm$.37	- 3.04 $\pm$.50	6.08
Speck	42.66 $\pm$.47	46.63 $\pm$.63	38.91 $\pm$.65	+ 7.72 $\pm$.91	8.48
bpr	27.35 $\pm$.24	30.44 $\pm$.34	24.06 $\pm$.32	+ 6.38 $\pm$.47	13.57
b vg	20.78 $\pm$.25	16.45 $\pm$.23	24.20 $\pm$.40	- 7.75 $\pm$.46	16.85
b a	21.71 $\pm$.26	20.11 $\pm$.36	23.17 $\pm$.37	- 3.06 $\pm$.52	5.88
b sp	31.09 $\pm$.24	32.36 $\pm$.35	29.97 $\pm$.31	+ 2.39 $\pm$.47	5.09
prvg	15.43 $\pm$.15	11.72 $\pm$.13	19.05 $\pm$.27	- 7.33 $\pm$.30	24.43
pr a	33.71 $\pm$.34	36.00 $\pm$.53	31.98 $\pm$.43	+ 4.02 $\pm$.68	5.91
pr sp	23.30 $\pm$.14	23.72 $\pm$.22	22.96 $\pm$.19	+ 0.76 $\pm$.29	2.62
asp	36.53 $\pm$.44	38.41 $\pm$.58	34.69 $\pm$.66	+ 3.72 $\pm$.88	4.23
bpr a	32.50 $\pm$.34	35.06 $\pm$.55	30.56 $\pm$.42	+ 4.50 $\pm$.69	6.52
bpr sp	27.25 $\pm$.29	31.22 $\pm$.45	24.45 $\pm$.37	+ 6.77 $\pm$.58	11.67
b asp	30.50 $\pm$.39	33.72 $\pm$.53	26.80 $\pm$.53	+ 6.92 $\pm$.75	9.22
pr asp	39.64 $\pm$.45	38.38 $\pm$.62	40.67 $\pm$.45	- 2.29 $\pm$.77	2.97
vgasp	18.97 $\pm$.37	12.81 $\pm$.26	25.20 $\pm$.61	-12.39 $\pm$.66	18.77
prvg sp	10.62 $\pm$.16	9.47 $\pm$.17	12.17 $\pm$.26	- 2.70 $\pm$.31	8.71
bprvga/	18.53 $\pm$.18	14.79 $\pm$.16	22.18 $\pm$.29	- 7.39 $\pm$.33	22.39
b vga/sp	16.70 $\pm$.25	13.97 $\pm$.26	19.56 $\pm$.41	- 5.59 $\pm$.49	11.40
bpr asp	22.92 $\pm$.28	22.65 $\pm$.42	23.11 $\pm$.38	- 0.46 $\pm$.57	.81

Table 6

A Comparison of the Mean Duration of Life of the Two Sexes

Stocks	Excess Duration of Life in Days	
	Males	Females
Black	.70 ± .74	>
Purple	5.59 ± .35	>
Speck	7.72 ± .91	>
Vestigial		< 6.00 ± .49
Arc		< 3.04 ± .50
Black Purple	6.38 ± .47	>
" Speck	2.39 ± .47	>
" Vestigial		< 7.75 ± .46
" Arc		< 3.06 ± .52
Purple Speck	0.76 ± .29	>
" Arc	4.02 ± .68	>
" Vestigial		< 7.33 ± .30
Arc Speck	3.72 ± .88	>
Black Purple Speck	6.77 ± .58	>
" " Arc	4.50 ± .69	>
" " Vestigial Arc/		< 7.39 ± .33
Black Arc Speck	6.92 ± .75	>
Purple Arc Speck		< 2.29 ± .77
Vestigial Arc Speck		< 12.39 ± .66
Purple Vestigial Speck		< 2.70 ± .31
Black Purple Arc Speck		< .46 ± .57
" Vestigial Arc/ Speck		< 5.59 ± .49
" Purple Vestigial Arc Speck		< 2.67 ± .30

The illuminating thing about the above comparison is that in black there is no significant difference in the duration of life of males and females, while there is in others. Combining black with any of the other mutants does not alter the relative difference in the sexes. In the case of black speck there is a considerable difference between the duration of life of the males and females from that of speck, seeming to imply that black while having no effect when alone or with purple,

vestigial, or arc, does have the effect of reducing the difference in speck. This effect of black on speck is consistent throughout, as will be noticed later on.

Purple with speck nullifies the effect of both in so far as increasing the difference in the duration of life of males and females. Purple with vestigial gives about the same effect as vestigial alone, indicating that vestigial overshadows any effects of purple in so far as the character in question is concerned. In purple arc the effect of purple is the dominant one.

In arc speck the result is almost the algebraic sum of the two. The greater mean duration of life is in the same direction as speck, which has the greater value.

If we continue our observations along the same line on the other combinations involving more than two mutants, the results are not materially different from those noted above. They are further complicated by interactions among themselves, however. For example: compare black purple vestigial, not pure for arc, ($< \varphi$ 7.39) with purple vestigial ($< \varphi$ 7.33); black purple arc ($< \delta$ 4.50) with purple arc ($< \delta$ 4.02); black arc speck ($< \delta$ 6.77) with arc speck ($< \delta$ 3.72), etc.

Other instances of the evidence of the effect of single characters when all others are common to both strains in question are: vestigial arc speck ($< \varphi$ 12.39) compared with arc speck ($< \delta$ 3.72), vestigial being ($< \varphi$ 6.00); black purple arc speck ($< \varphi$.46) with vestigial black purple arc speck ($< \varphi$ 2.67).

In other cases when the mutants involved have specific interactions among themselves, the results are not as regular from the mathematical point of view. As in black purple speck, ($< \delta$ 6.77) as compared with purple speck ($< \delta$ 0.76). We have noted before this the irregular behavior of speck combinations with either black or purple.

This instance in *Drosophila* where a character has a different expression in the two sexes, without this involving necessarily any difference in the sex chromosomes is not at all new. Bridges and Morgan (17) and Lynch (20) give an account of differential

fertility in various mutant stocks of *Drosophila*. The females of "rudimentary" and "fused" wings in the first chromosome, "morula" and "reduced bristle" in the second, and "dwarf" in the third are infertile, while the males are fully fertile. The case is reversed in "cleft" wings of the first chromosome where the males are fertile and the females infertile.

Cases of differential fertility are by no means the rule in the first chromosome, and such instances as have been noted above can only be conceived as being effects of the mutants per se. Then of course we have the general phenomenon of non-crossing over in the male.

Two other cases of sexual differences in the expression of a character where genes are in autosomal chromosomes have come to the notice of the writer. As these data are as yet unpublished no further mention can be made here. All we are interested in showing at present, is that these sex differences in duration of life have a parallel in the literature of *Drosophila*. The basic cause of these differences may or may not be the same.

Inheritance of Duration of Life in Males.

Since sex does not affect duration of life uniformly in one direction in the different strains involved in these studies, it is deemed advisable to study the two sexes separately and thus eliminate an item which will obviously complicate the interpretation of results and mask or accentuate differences through its alternating differential effect.

Table 7 gives the survivors in the male line of the parent stocks and the five mutants. These figures are not very different from those in Table 4 which give the survivors for the whole population. Due to the differential effect of sex the relative position of arc and purple are reversed. These two characters, however, have about the same duration of life and this difference should not prove important. Fig. 3 shows the data in Table 7 graphically. The survivorship data for the different combinations are given in Tables 8 and 9.

Table 7

Survivorship Distribution of Males of Original Stocks and Strains
Involving Single Mutations.

Age in Days	Number of Survivors up to Indicated Age						
	Wild	Quintuple	Black	Purple	Vestigial	Arc	Speck
1	1000	1000	1000	1000	1000	1000	1000
4	998	953	994	994	1000	990	990
7	998	655	991	958	922	921	987
10	984	356	976	904	727	837	980
13	968	173	976	836	563	751	960
16	937	85	961	771	384	688	934
19	912	144	943	706	273	628	924
22	879	22	896	654	184	573	897
25	854	19	863	602	73	516	877
28	821	11	839	537	24	393	854
31	757	0	764	448	8	343	824
34	716	-	678	302	0	283	784
37	541	-	606	222	-	230	751
40	429	-	504	155	-	165	728
43	327	-	427	107	-	118	651
46	223	-	367	59	-	79	571
49	129	-	290	37	-	36	525
52	105	-	248	13	-	17	415
55	71	-	218	4	-	0	332
58	59	-	131	1	-	-	262
61	50	-	78	0	-	-	196
64	39	-	45	-	-	-	136
67	29	-	27	-	-	-	76
70	20	-	24	-	-	-	37
73	12	-	3	-	-	-	20
76	2	-	3	-	-	-	0
79	0	-	0	-	-	-	-

Abs.No.of flies	560	365	335	944	245	417	301
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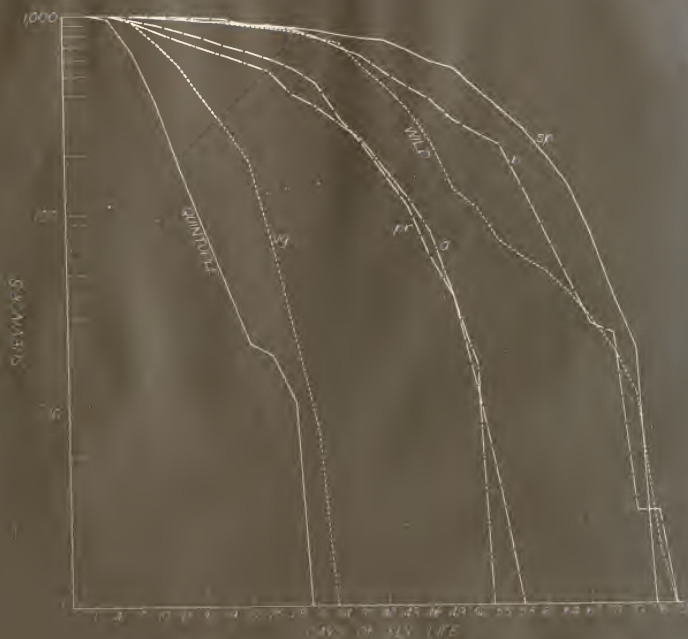


Fig. 3. Survivorship graphs of original stocks and single mutants. Males.

Table 8

Survivorship Distribution of Males of Strains Involving Two Mutations

Age in Days	Number of Survivors up to Indicated Age							
	bpr	b vg	b a	b sp	prvg	pr a	pr sp	asp
1	1000	1000	1000	1000	1000	1000	1000	1000
4	997	993	986	996	972	992	973	994
7	971	974	907	983	901	978	924	984
10	924	876	825	962	611	944	832	968
13	887	707	724	949	336	915	745	949
16	832	472	565	922	146	871	691	911
19	763	280	463	864	67	813	623	879
22	717	163	355	763	28	748	554	822
25	656	94	276	687	11	666	463	784
28	582	55	227	617	2	610	364	746
31	492	26	180	532	0	545	282	686
34	418	7	136	470	-	485	205	600
37	336	3	100	379	-	457	151	537
40	264	0	68	282	-	412	100	495
43	184	-	30	201	-	384	61	441
46	131	-	14	159	-	338	34	371
49	75	-	12	87	-	292	24	289
52	44	-	5	61	-	217	15	216
55	19	-	2	27	-	169	12	127
58	9	-	0	8	-	135	9	67
61	6	-	-	4	-	97	4	48
64	3	-	-	2	-	64	3	29
67	1	-	-	0	-	33	2	13
70	0	-	-	-	-	0	1	3
73	-	-	-	-	-	-	1	3
76	-	-	-	-	-	-	0	3
79	-	-	-	-	-	-	-	3
82	-	-	-	-	-	-	-	3
85	-	-	-	-	-	-	-	0
Abs.No.of flies	697	307	428	528	563	497	1465	315

Table 9

Survivorship Distribution of Males of Strains Involving
Three and Four Mutations

Age in Days	Number of Survivors up to Indicated Age									
	bpr a	bpr sp	b asp	pr asp	vgasp	prvg	sp bpr	vga/ b	vga/sp	bpr asp
1	1000	1000	1000	1000	1000	1000	1000	1000	1000	1000
4	995	988	990	997	990	978	995	972	975	
7	978	956	974	979	864	659	940	881	925	
10	947	924	939	949	617	315	800	672	830	
13	896	866	904	918	362	123	595	456	753	
16	852	819	865	888	206	18	353	313	655	
19	804	764	843	849	167	11	202	194	573	
22	760	722	798	834	111	7	95	153	470	
25	695	678	737	795	56	7	52	97	370	
28	646	627	625	731	28	4	32	59	295	
31	569	556	577	665	17	4	22	22	230	
34	496	479	513	556	7	4	7	6	187	
37	448	389	458	502	3	4	3	0	150	
40	375	315	388	459	3	4	2	-	117	
43	320	201	301	420	3	4	0	-	73	
46	276	134	224	344	0	0	-	-	50	
49	240	86	160	299	-	-	-	-	27	
52	194	51	74	236	-	-	-	-	13	
55	123	21	22	184	-	-	-	-	10	
58	92	9	13	136	-	-	-	-	7	
61	75	5	0	100	-	-	-	-	5	
64	31	2	-	66	-	-	-	-	0	
67	29	2	-	42	-	-	-	-	-	
70	10	0	-	9	-	-	-	-	-	
73	0	-	-	3	-	-	-	-	-	
76	-	-	-	0	-	-	-	-	-	
Abs.No.of flies	413	432	312	331	287	276	600	320	400	

Examining Table 10 (Biometric Constants) we find that the mean duration of life of black of $41.03 \pm .53$ days and that of speck of $46.63 \pm .63$ is higher than that of the wild stock, which is only 38.08 days. The difference between wild and black of $2.95 \pm .64$ days is not big but that between wild and speck, $8.55 \pm .72$ looks rather important. There is a suggestion in this of the presence of a factor that increases the duration of life. Fig 3 shows this rather clearly. Purple and arc give a lower duration of life than the wild stock, and vestigial still lower.

Table 10

Biometric Constants for Duration of Life of Different Strains

of Male Drosophila.

Strains	Number of flies	Mean (in days)	Standard deviation (in days)	Coefficient of Variation
Wild	560	38.08 ± .36	12.74 ± .26	33.46 ± .75
bprvgasp				
Quintuple	365	9.45 ± .17	4.75 ± .12	50.26 ± 1.63
b	335	41.03 ± .53	14.35 ± .37	34.99 ± 1.02
pr	944	27.42 ± .27	12.28 ± .19	44.79 ± .82
vg	245	14.98 ± .28	6.41 ± .20	42.80 ± 1.52
a	417	25.20 ± .33	9.87 ± .23	39.17 ± 1.05
sp	301	46.63 ± .63	16.21 ± .45	34.76 ± 1.06
bpr	697	30.44 ± .34	13.19 ± .24	43.32 ± .92
b vg	307	16.45 ± .23	6.09 ± .17	37.02 ± 1.14
b a	428	23.17 ± .37	11.80 ± .26	50.93 ± 1.39
b sp	528	32.36 ± .35	12.09 ± .25	37.35 ± .88
prvg	568	11.72 ± .13	4.49 ± .09	38.31 ± .87
pr a	497	36.00 ± .53	17.42 ± .37	48.40 ± 1.25
pr sp	1465	23.72 ± .22	12.45 ± .16	52.48 ± .81
asp	315	38.41 ± .58	15.15 ± .41	39.44 ± 1.21
bpr a	413	35.06 ± .55	16.43 ± .39	46.86 ± 1.32
bpr sp	432	31.22 ± .45	13.73 ± .32	43.97 ± 1.19
b asp	312	33.72 ± .53	13.75 ± .37	40.78 ± 1.27
pr asp	331	38.38 ± .62	16.63 ± .44	43.32 ± 1.33
vgasp	287	12.81 ± .26	6.43 ± .18	50.17 ± 1.73
prvg sp	276	9.47 ± .17	4.30 ± .12	45.39 ± 1.55
bprvga/	600	14.79 ± .16	5.86 ± .11	39.61 ± .88
b vga/sp	320	13.97 ± .26	7.02 ± .19	50.26 ± 1.64
bpr asp	400	22.65 ± .42	12.42 ± .30	54.84 ± 1.66

Since we have data for so many combination, the results are difficult to interpret when en masse. Close observation has revealed an order which we now propose to test out. Let us assume for the moment that each of the five characters studied has a definite duration of life inherent to it, in the same manner as other characters of Drosophila known to control externally

visible characters are by common observation conceded as being of low or good vitality, poor in fertility or fully fertile, etc. There is the other possibility of taking duration of life as a separate character represented by a gene or genes in the chromosome, closely linked to some or all of the characters studied. As the discussion that follows will not be affected one way or the other whichever of the two views is taken, we will leave this for the present as an open question.

We will first test the reaction of the different mutants with one another as to their duration of life.

Combining black with each of the others we have:

Table 11

Strain	Mean Duration of Life	Strain	Mean Duration of Life	Difference
Black	41.02 ± .53			
Purple	27.42 ± .27	Black Purple	30.44 ± .34	+ 3.02 ± .43
Vestigial	14.98 ± .28	" Vestigial	16.45 ± .23	+ 1.47 ± .36
Arc	25.20 ± .33	" Arc	20.11 ± .36	- 5.09 ± .49
Speck	46.63 ± .63	" Speck	32.36 ± .35	- 14.27 ± .72

From the above we can see that black was instrumental in raising the value of purple and vestigial when it combines with them. It lowered the value of arc and speck. The combination value in two cases, is intermediate between that of the single mutations. In the other two cases it is lower than either component. See figures 4 and 5.

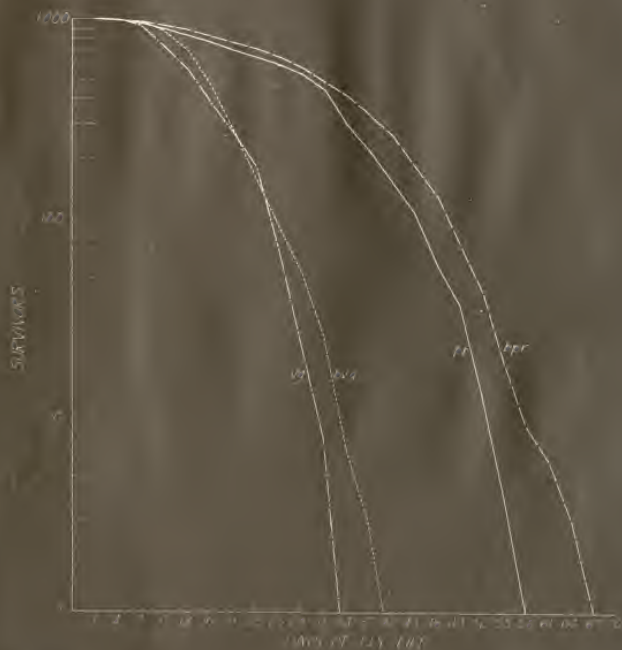


Fig. 4. Male l_x lines comparing bpr with pr, and b vg with vg.

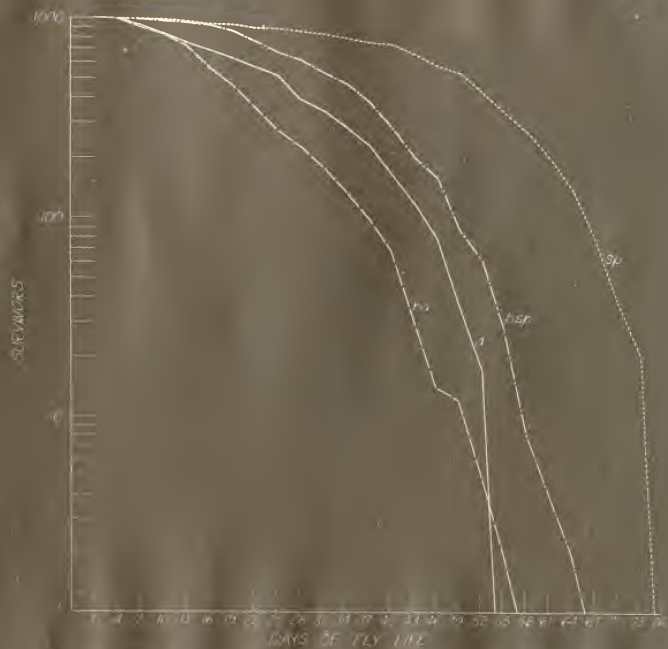


Fig. 5. Male 1_x lines comparing $\underline{b}$ sp with sp, and $\underline{b}$ a with $\underline{a}$.

Combining purple with the others we have:

Table 12

Strain	Mean Duration of Life	Strain	Mean Duration of Life	Difference
Purple	27.42 ± .27			
Black	41.02 ± .53	Purple Black	30.44 ± .34	- 10.58 ± .63
Vestigial	14.98 ± .28	" Vestigial	11.72 ± .13	- 3.26 ± .31
Arc	25.20 ± .33	" Arc	36.00 ± .53	+ 10.80 ± .62
Speck	46.63 ± .63	" Speck	23.72 ± .22	- 22.91 ± .67

In this case purple raised the value of arc (or vice versa) and lowered that of black, vestigial, and speck. In only a single instance in the above is the combination value intermediate.

Combining vestigial with the others we have:

Table 13

Strain	Mean Duration of Life	Strain	Mean Duration of Life	Difference
Vestigial	14.98 ± .28			
Black	41.02 ± .53	Vestigial Black	16.45 ± .23	- 24.57 ± .58
Purple	27.42 ± .27	" Purple	11.72 ± .13	- 15.70 ± .30
Arc Speck	38.41 ± .58	" Arc Speck	12.81 ± .26	- 25.60 ± .64

Vestigial black is the only combination intermediate between that of the single mutants above. Both vestigial purple and vestigial arc speck have lower values than their components. It was not practicable to make combinations with arc and speck separately due to the masking effect of vestigial on arc. In every case above vestigial reduced the value of the other character in the combination.

From the foregoing it is evident that the duration of life of combinations is not always, nor even generally, the average of the single mutants entering into it. Also, that there is interaction between different mutants which seems to be definite, if correctly understood or interpreted.

The differences noted above are all significant from the standpoint of probability. The least significant difference noted is four times its probable error (see vestigial vs. black vestigial). However, since we are dealing with extremely variable material (see table of biometric constants) and in all sorts of combinations, it is best not to attach undue importance to small differences in order that we may appreciate the meaning of the larger differences.

Some facts are outstanding from the data presented above which we now propose to examine further.

1. Whenever vestigial is at all present in a strain the value of the combination is about the same or lower than that of vestigial alone. This further reduction seems to be dependent on other mutants present other than vestigial, purple and speck. Black raises the value of vestigial to a slight extent

Table 14

Strains	Mean Duration of Life	Difference
Vestigial	14.98 ± .28	
Black, Vestigial	16.45 ± .23	+ 1.47 ± .36
Purple, Vestigial	11.72 ± .13	- 3.26 ± .31
Black, Purple, Vestigial, Arc/,	14.79 ± .16	- .19 ± .32
Vestigial, Arc, Speck	12.81 ± .26	- 2.17 ± .38
Black, Vestigial, Arc/, Speck	13.97 ± .26	- 1.01 ± .38
Purple, Vestigial, Speck	9.47 ± .17	- 5.51 ± .33
Black, Purple, Vestigial, Arc, Speck	9.45 ± .17	- 5.53 ± .33

Vestigial then may be recognized as the most powerful single factor in determining duration of life among the mutants studied. It overshadows the

effect of the other characters, although its dominance, if such we may call it, is not complete. See Figs. 6 and 7



Fig. 6. Male 1_x lines of stocks containing vestigial.
Two mutations.



Fig. 7. Male l_x lines of stocks containing vestigial.
Three or more mutants.

2. Whenever vestigial is absent , purple is the dominant factor; that is, when in combination with the other mutants, it tends to either raise or lower the value of the combination to its level. See Fig. 8.

Table 15

Strains	Mean Duration of Life	Difference
Purple	<u>27.42 ± .27</u>	
Black, Purple	30.44 ± .34	+ 3.02 ± .43
Purple, Arc	36.00 ± .53	+ 8.58 ± .60
Purple, Speck	23.72 ± .22	- 3.70 ± .35
Black, Purple, Arc	35.06 ± .55	+ 7.64 ± .61
Black, Purple, Speck	31.22 ± .45	+ 3.80 ± .52
Purple, Arc, Speck	38.38 ± .62	+ 10.96 ± .68
Black, Purple, Arc, Speck	22.65 ± .42	- 4.77 ± .50

Purple is sensibly modified by black and arc, specially the latter, which tends to raise its value. Speck on the other hand has little effect on purple. The effect of arc on purple is a little unusual, since arc by itself has a lower mean duration of life than purple.

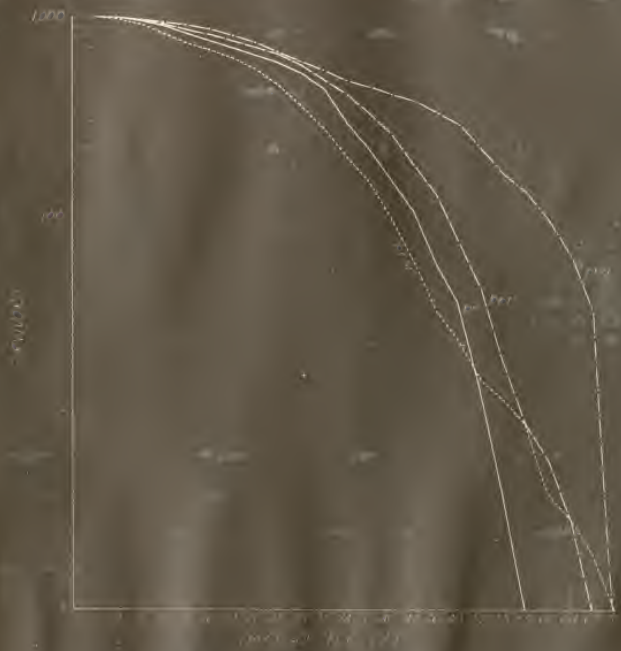


FIG. 8. Male 1_x lines of stocks containing purple combinations, without vestigial.

3. Arc, while recessive in general, is a strong modifier of the values of the other mutants. It increases the value of purple and lowers that of black and speck.

Table 16

Strains		Original Strain + Arc		Difference
pr	27.42 ± .27	pr a	36.00 ± .53	+ 8.58 ± .60
bpr	30.44 ± .34	bpr a	35.06 ± .55	+ 4.62 ± .65
pr sp	23.72 ± .22	pr asp	38.38 ± .62	+ 14.66 ± .66
vg	14.98 ± .28	vgasp	12.81 ± .26	- 2.17 ± .38
bpr sp	31.22 ± .45	bpr asp	22.65 ± .42	- 8.57 ± .61
b	41.03 ± .53	b a	20.11 ± .36	- 20.92 ± .64
sp	46.63 ± .63	asp	38.41 ± .58	- 8.22 ± .86
b sp	32.36 ± .35	b asp	33.72 ± .53	+ 1.36 ± .64

4. As between black and speck, when alone they represent long duration of life, longer in fact than the wild males. In combination the resulting strain has a lower duration of life than either component mutant. See Fig. 9. Their reaction with other mutants has already been noted in the individual discussion of such mutants.

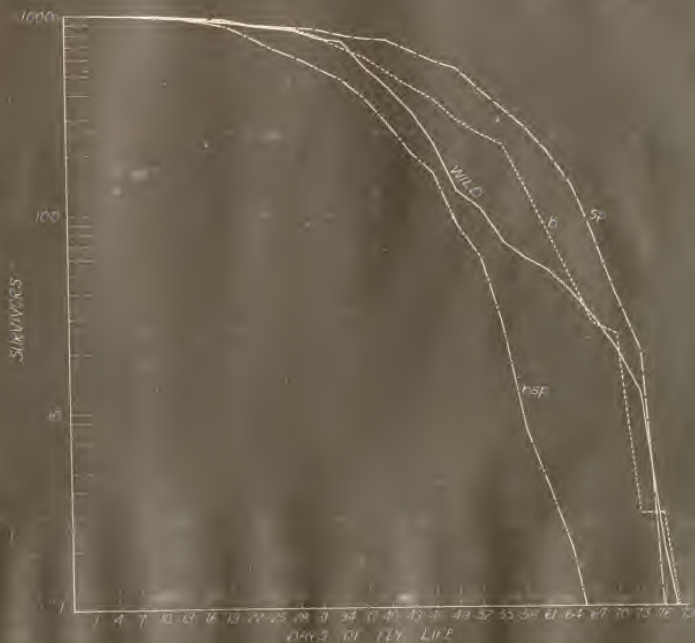


Fig. 9. Male l_x lines of b and sp compared with wild and their combination b sp .

Inheritance of Duration of Life in Females.

Duration of life in the females should not differ materially from that of males after due correction is made for the difference in influence of sex, if the behavior of the factor involved is definite. In other words, should we plot the survivorship lines of males and females of the same strain, they should run virtually parallel to each other, maintaining a distance equal to the difference due to sex, but otherwise describing the same type of curve.

We shall test this for the five single mutants.

Our data in Table 6 shows us that in:

Black - there is a non-significant difference between males and females of	0.70 ± .74 days
Purple - males are longer lived by	5.59 ± .35 "
Vestigial - females are longer lived by	6.00 ± .49 "
Arc - females are longer lived by	3.04 ± .50 "
Speck - males are longer lived by	7.72 ± .91 "

Figures 10 and 11 show that our assumption as to the effect of sex is essentially correct for black, purple, vestigial, and speck. The case of arc is a little different. In this there is a heavy mortality of males in early and later life and a low one in middle life. The case is reversed in the females, with the result that the curves cross and re-cross each other. This behavior of arc is felt more or less in some of its combinations as may be seen from Figs. 12 and 13 but not sufficiently to modify the general results. This characteristic of arc, together with its property of being recessive in general yet a powerful modifier, as pointed out in the discussion of duration of life in males, suggests the possibility of its being a gene, or modifier, or property of a gene different in nature from the other mutations studied.

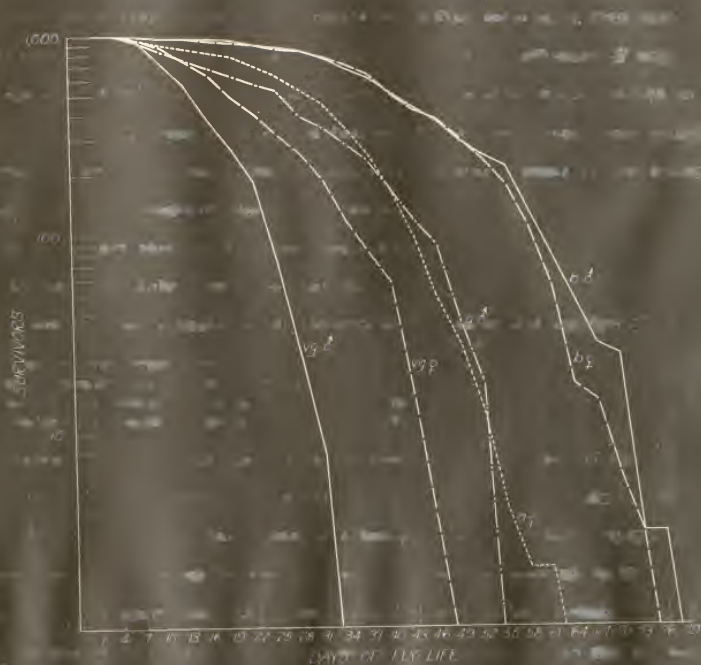


Fig. 10. Survivorship lines of b, a, and vg, males and females compared.

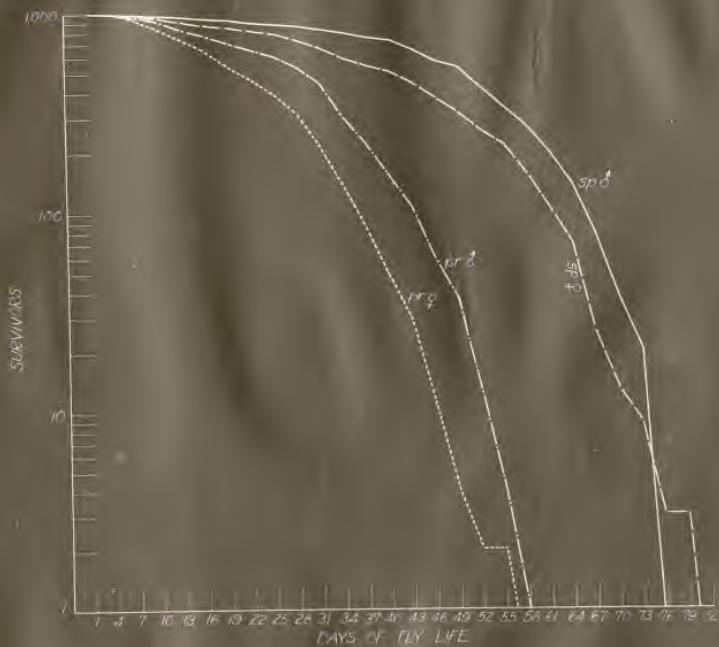


Fig. 11. Survivorship lines of *pr* and *sp*, males and females compared.

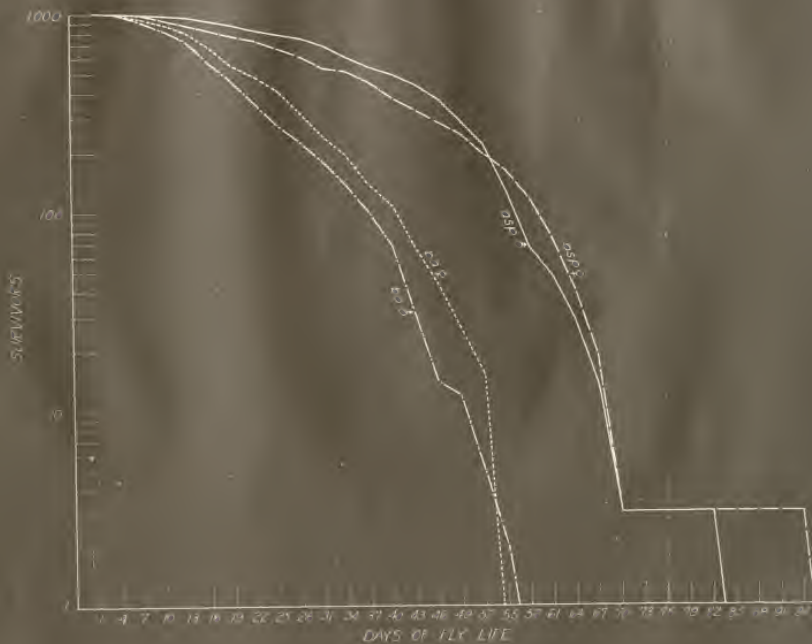


Fig. 12. Survivorship lines of arc combinations, asp and asp, showing irregularity of course of male and female lines.

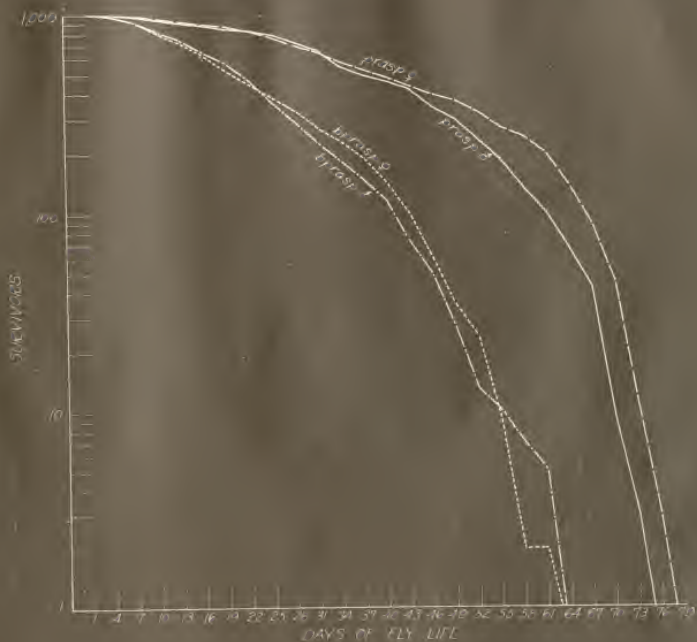


Fig. 13. Survivorship lines of arc combinations, *pr asp* and *bpr asp*, showing irregularity of male and female lines.

The survivorship data of the different female strains are given in Tables 17, 18 and 19, the distributions being on the basis of a 1000 as in all previous tables.

Table 17

Survivorship Distribution of Females of Original Stocks and

Strains Involving Single Mutations.

Age in Days	Number of Survivors up to Indicated Age						
	Wild	Quintuple	Black	Purple	Vestigial	Arc	Speck
1	1000	1000	1000	1000	1000	1000	1000
4	997	957	989	996	993	983	981
7	987	707	983	921	951	953	969
10	960	483	972	844	878	904	947
13	932	352	963	749	750	868	906
16	871	240	938	655	649	823	868
19	857	176	913	543	497	781	846
22	842	121	885	468	410	704	814
25	812	74	845	395	319	628	780
28	780	48	825	319	257	528	733
31	731	24	772	235	187	455	670
34	695	12	701	139	115	345	594
37	635	10	631	84	80	251	541
40	593	2	501	48	56	164	506
43	504	0	414	29	14	98	443
46	441	-	375	11	3	47	371
49	345	-	296	4	0	28	314
52	268	-	234	2	-	13	255
55	154	-	175	2	-	4	217
58	112	-	107	0	-	2	154
61	81	-	54	-	-	2	104
64	50	-	17	-	-	0	69
67	34	-	14	-	-	-	25
70	21	-	6	-	-	-	13
73	4	-	3	-	-	-	9
76	0	-	0	-	-	-	3
79	-	-	-	-	-	-	3
82	-	-	-	-	-	-	0
Abs. No. of flies	676	420	355	1006	288	470	318

Table 18

Survivorship Distribution of Females of Strains Involving Two Mutations

Age in Days	Number of Survivors to Indicated Age							
	bpr	b vg	b a	b sp	prvg	pr a	pr sp	asp
1	1000	1000	1000	1000	1000	1000	1000	1000
4	990	982	981	992	981	1000	967	994
7	943	969	938	978	931	969	919	972
10	807	912	878	962	836	929	839	919
13	722	820	800	942	706	893	757	869
16	638	735	680	899	566	819	673	816
19	577	647	556	842	436	752	608	769
22	526	536	489	759	335	683	527	732
25	459	451	416	634	245	603	433	670
28	390	363	318	531	203	535	338	611
31	319	291	242	453	149	465	265	539
34	255	209	193	371	82	400	192	508
37	196	147	137	275	33	342	141	452
40	141	90	109	178	11	304	83	377
43	97	46	67	116	4	258	43	330
46	62	15	43	90	2	227	22	283
49	32	8	26	67	0	189	8	249
52	24	8	15	53	-	140	5	196
55	5	5	0	13	-	104	2	162
58	4	0	-	3	-	83	0	118
61	1	-	-	0	-	57	-	75
64	1	-	-	-	-	49	-	40
67	0	-	-	-	-	28	-	19
70	-	-	-	-	-	0	-	3
73	-	-	-	-	-	-	-	3
76	-	-	-	-	-	-	-	3
79	-	-	-	-	-	-	-	3
82	-	-	-	-	-	-	-	3
85	-	-	-	-	-	-	-	3
88	-	-	-	-	-	-	-	3
91	-	-	-	-	-	-	-	3
94	-	-	-	-	-	-	-	3
97	-	-	-	-	-	-	-	0
Abs.No. of flies	787	388	466	601	523	652	1750	321

Table 19

Survivorship Distribution of Females of Strains Involving

Three and Four Mutations.

Age in Days	Number of Survivors up to Indicated Age								
	bpr a	bpr sp	b asp	pr asp	vgasp	prvg sp	bprvg/a	b vga/sp	bpr asp
1	1000	1000	1000	1000	1000	1000	1000	1000	1000
4	995	966	985	997	986	974	989	974	977
7	976	910	963	992	939	801	953	886	922
10	920	833	885	963	842	540	880	804	819
13	862	732	826	928	710	354	776	693	733
16	808	655	741	902	620	189	687	562	637
19	753	595	674	875	559	126	565	454	533
22	700	532	615	832	509	83	458	363	451
25	638	486	537	774	455	56	367	288	384
28	552	401	456	702	409	36	287	206	333
31	449	346	378	649	380	33	211	160	274
34	378	264	326	582	312	17	157	108	234
37	308	215	267	527	247	10	114	82	193
40	256	152	189	487	183	3	67	52	146
43	199	95	126	434	133	0	26	26	102
46	164	54	78	396	104	-	5	16	61
49	124	40	41	367	97	-	3	10	35
52	94	22	15	322	54	-	3	3	24
55	61	11	0	269	29	-	2	0	9
58	49	3	-	242	25	-	2	-	2
61	35	2	-	199	11	-	2	-	2
64	28	2	-	138	4	-	2	-	0
67	23	0	-	88	0	-	2	-	-
70	12	-	-	45	-	-	2	-	-
73	3	-	-	11	-	-	2	-	-
76	0	-	-	3	-	-	2	-	-
79	-	-	-	0	-	-	0	-	-
Abs. No. of flies	574	624	270	376	279	302	616	306	576

The frequency constants are given in Table 20.

Table 20

Biometric Constants for Duration of Life of Different

Strains of Female *Drosophila*.

Strains	Number of flies	Mean (in days)	Standard Deviation (in days)	Coefficient of Variation
Wild	676	40.62 ± .42	16.14 ± .30	39.74 ± .84
bprvgasp (Quintuple)	420	12.12 ± .25	7.50 ± .17	61.90 ± 1.91
b	355	40.33 ± .51	14.20 ± .36	35.20 ± 1.00
pr	1006	21.83 ± .23	10.76 ± .16	49.30 ± .90
vg	288	20.98 ± .40	9.95 ± .28	47.45 ± 1.61
a	470	28.24 ± .37	11.89 ± .26	42.09 ± 1.08
sp	318	38.91 ± .65	17.32 ± .46	44.52 ± 1.41
bpr	787	24.06 ± .32	13.33 ± .23	55.39 ± 1.20
b vg	388	24.20 ± .40	10.78 ± .26	44.56 ± 1.28
b a	466	23.17 ± .37	11.30 ± .26	50.93 ± 1.39
b sp	601	29.97 ± .31	11.44 ± .22	38.18 ± .84
prvg	523	19.05 ± .27	9.27 ± .19	48.65 ± 1.23
pr a	652	31.93 ± .43	16.36 ± .31	51.15 ± 1.18
pr sp	1750	22.96 ± .19	11.68 ± .13	50.89 ± .71
asp	321	34.69 ± .66	17.55 ± .47	50.58 ± 1.66
bpr a	574	30.56 ± .42	14.99 ± .30	49.05 ± 1.19
bpr sp	624	24.45 ± .37	13.59 ± .26	55.59 ± 1.35
b asp	270	26.30 ± .53	12.95 ± .38	48.32 ± 1.70
pr asp	376	40.67 ± .45	18.14 ± .64	45.34 ± 1.33
vgasp	279	25.20 ± .61	15.11 ± .43	59.95 ± 2.24
prvg ap	302	12.17 ± .26	6.77 ± .19	55.61 ± 1.94
bprvga/	616	22.18 ± .29	10.64 ± .20	47.95 ± 1.11
b vga/sp	306	19.56 ± .41	10.75 ± .29	54.95 ± 1.90
bpr asp	576	23.11 ± .38	13.37 ± .27	57.85 ± 1.49

Using the same method of examination as in males, we have:

Table 21

Strains	Mean Duration of Life	Difference
Vestigial	20.98 ± .40	
Black, Vestigial	24.20 ± .40	+ 3.22 ± .57
Purple, Vestigial	19.05 ± .27	- 1.93 ± .48
Black, Purple, Vestigial, Arc/	22.18 ± .29	+ 1.20 ± .49
Vestigial, Arc, Speck	25.20 ± .61	+ 4.22 ± .73
Black, Vestigial, Arc/Speck	19.56 ± .41	- 1.42 ± .57
Purple, Vestigial, Speck	12.17 ± .26	- 8.81 ± .48
Black, Purple, Vestigial, Arc, Speck	12.12 ± .25	- 8.86 ± .47

The above table shows that the results with vestigial in the female are on the whole the same as those in the male; that is, vestigial operated to reduce the values of the mutants with which it has entered into combination to its general level. There is considerable variation, though as its effects are modified to a great extent by the other mutants as in the case of the males. Purple and speck tend to reduce the duration of life of the combinations further, while black tends to raise it. The effect of arc in the male was not significant, but in this case as already pointed out the comparatively much longer life of female arcs as compared with male arcs in early life, makes its influence felt in the combination.

below

The table shows the effect of purple on the other mutants whenever vestigial is absent.

Table 22

Strains	Mean Duration of Life	Difference
Purple	21.83 ± .23	
Black, Purple	24.06 ± .32	+ 2.23 ± .39
Purple, Arc	31.98 ± .43	+ 10.15 ± .49
Purple, Speck	22.96 ± .19	+ 1.13 ± .30
Black, Purple, Arc	30.56 ± .42	+ 8.73 ± .48
Black, Purple, Speck	24.45 ± .37	+ 2.62 ± .44
Purple, Arc, Speck	40.67 ± .45	+ 18.84 ± .51
Black, Purple, Arc, Speck	23.11 ± .38	+ 1.28 ± .45

As in the males the effect of purple is not as pronounced as vestigial, being modified considerably by the other mutations. The direction of these modifications is consistent with that found in the males. Black, and especially arc raise its value while speck, without a third character, has little effect. See Figures 14 and 15.

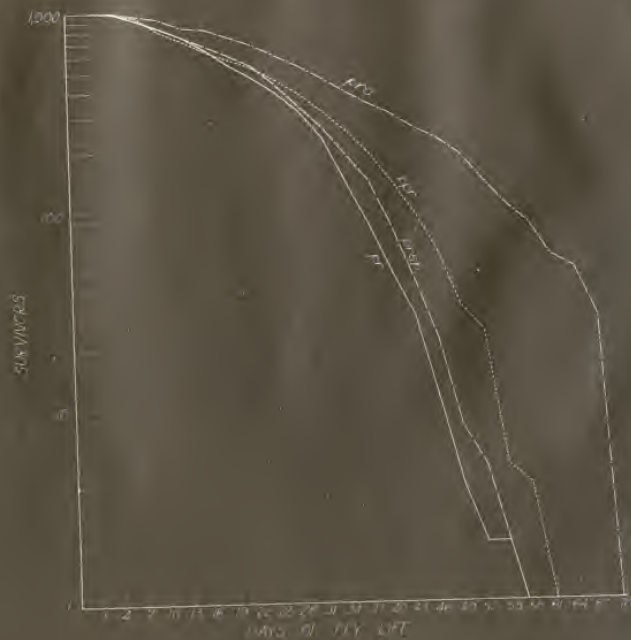


Fig. 14. Female l_x lines of purple combinations. Two mutations.

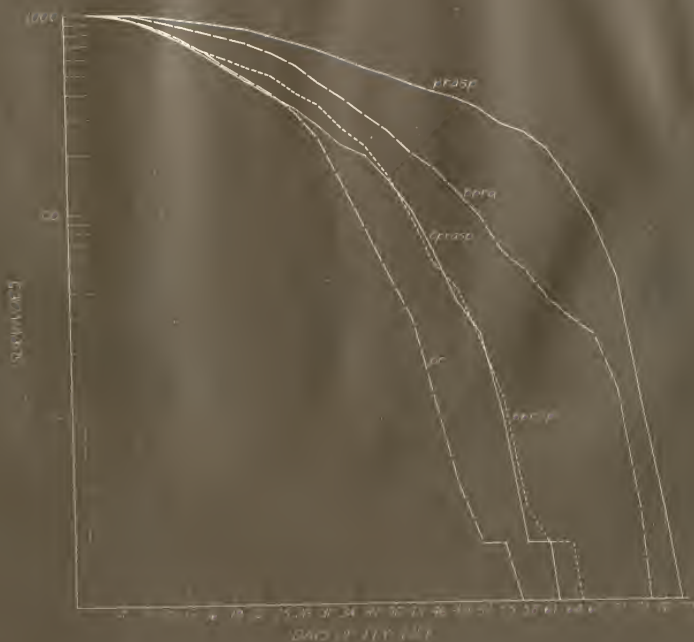


Fig. 15. Female l_x lines of purple combinations. Three or more mutations.

Arc also acts as a recessive in general, in the sense that it does not bring the value of its combinations to its level, but as in the male it increases the value of purple and vestigial and lowers that of black and speck. The following table is illuminating on this point.

Table 23

Strain		Strain + arc		Difference
pr	21.83 * .23	pr a	31.98 * .43	+ 10.15 * .49
bpr	24.06 * .32	bpr a	30.56 * .42	+ 6.50 * .53
pr sp	22.96 * .19	pr asp	40.67 * .45	+ 17.71 * .49
vg	20.93 * .40	vgasp	25.20 * .61	+ 4.22 * .73
bpr sp	24.45 * .37	bpr asp	23.11 * .38	- 1.34 * .53
b	40.33 * .51	b a	23.17 * .37	- 17.16 * .63
sp	38.91 * .65	asp	34.69 * .66	- 4.22 * .93
b sp	29.97 * .31	b asp	26.80 * .53	- 3.17 * .61

Black and speck, individually, have as high a duration of life as the wild stock. The two in combination give a lower duration of life than either of them alone. They may be considered as recessives in the sense that their combinations follow the general level of duration of life of the other character rather than theirs. When not together, however, they have the tendency of raising the duration of life of the combination in which they take part above that of the other mutant when alone.

Discussion of Results.

As a first attempt in the localization of the gene or genes governing duration of life these experiments have perhaps been more successful in outlining future lines of endeavor by having demonstrated that certain phenomena likely to be supposed to be concerned with duration of life have no influence over it at all. A number of theories have come to the mind of the writer during the course of these experiments, suggested mostly by the general behavior of factors already well understood. A brief mention of these will be made, as by a process of elimination of what duration of life is not, we may be led closer and closer to the narrower path of what it is.

1. Influence of Number of "Irregular Links". Mutations by their nature and the circumstances of their appearance may be considered as due to "abnormal" genes. If we accept Morgan's theory of linear arrangement of genes, and picture the chromosomes as consisting of a string of "beads", each representing a gene, it is easy to conceive of an "abnormal bead" coming in forming a weak link on both sides of it. If each irregular link should affect duration of life adversely, we would expect a corresponding shortening of the duration of life with the addition of each mutant gene. In other words, the number of irregular links being directly dependent on the number of these new genes, the duration of life of the resulting strain should be inversely proportional to the number of mutations it has. Our results have shown that there is no foundation for this belief, as the number of mutant genes in a strain per se has no relation to its duration of life.

2. Influence of Number of Mutations. Similarly, it is of common observation that mutants in general are not as viable, nor as fertile, nor as long lived as the wild stocks of *Drosophila*. The wild stock has been regarded as the standard, and the addition of any mutation generally lowers this standard.

Sometimes it does not affect it, but I have not seen of a case recorded of a mutation affecting fertility and duration of life positively. According to the above an increase in the number of mutations in a chain should be followed by a corresponding reduction in the vital properties of the individuals. Our data shows that duration of life depends not so much on the number of mutations in a strain, but rather on the intrinsic property of the mutations present in it.

3. Blending Effects of Mutants. If a number of mutant genes are known to affect duration of life definitely and yet are independent of each other, one may conceive of their behaving in this fashion: (a) The resulting combination of two or more mutants would give a duration of life which is the average of the components; or (b) if each mutant may be regarded as increasing or decreasing duration of life so many days from the standard, a combination strain would give the algebraic sum of the value of each mutation with the normal duration of life. Neither of these alternatives is supported by the results. A good illustration is found in the case of black and speck. Individually they have no effect, or rather increase duration of life over that of the wild strain; in combination they shorten duration of life.

4. Physiological Effect of Mutants. Among the mutants studied vestigial has the greatest effect on duration of life, and it so happens that it is the external character that affects most the general behavior of the fly by curtailing its normal activity. One may easily construe that it is this physical defect, if we may regard it as so, that is the direct cause of the shortening of the duration of life of those strains containing the character vestigial. This view has been demonstrated by Pearlet al(21) to be erroneous. The duration of life of wild flies the wings of which were clipped was compared with normal ones. The results show a slightly longer duration of life in the normal ones, but not sufficient to account for the big difference between normal and vestigial. This small difference may properly be attributed to the injury

caused to the flies in handling and clipping their young wings and in causing an open wound in the veins severed.

If further proof is necessary on this point, we have the case of purple. This is a mutation affecting eye color, which in so far as it is possible to observe, has no other effect in the physical make up of the flies, and yet it affects duration of life to a very marked extent.

There is therefore a more fundamental reason for the difference in the duration of life of these mutants.

What then is the possible explanation?

In examining our data critically we are forced to conclude that the different mutants whose duration of life has been the object of this study behave as units in so far as this character is concerned. This behavior is as distinct and regular as the external appearance of the character which serves as an "earmark" for the identification of the gene in which each is located.

The question now is whether they are located in the very gene of each of the mutants studied or whether they are separate genes, completely or very closely linked to these mutant genes. It is not probable that five mutations picked at random as subjects for this study should develop, each and every one of them, to be linked to a determiner for duration of life. We have had several years experience in the laboratory with vestigial stock, which contains the factor affecting duration of life most, pure and crosses, and involving several thousand individuals, and we have yet to find a vestigial fly living beyond the regular span established by this character. If the gene for duration of life were distinct, we would expect a certain proportion of long lived vestigial flies due to cross overs, small as the proportion may be. The assumption, therefore, that ^{the} duration of life factors recognized reside in the

very genes of the mutants studied seems to be the more plausible and logical.

Morgan and his students have found about fifty factors that affect eye color alone. In this one attempt at an apparently more complicated character, at five random mutants, they were all found to affect duration of life. It is not too much to presume that there are many more.

We have called attention to the fact that there is an appreciable dominance of certain genes over others in respect of effect upon duration of life. Such effects may be construed as of the same nature as the effects produced by the presence of a number of factors controlling the same organ but located in different parts of a chromosome or even in different chromosomes. Numerous examples are found in the mutant eye colors and wing lengths of *Drosophila*. Sometimes there is complete dominance, as the case of vestigial hiding the presence of arc absolutely; sometimes there is blending, as the effect of vermillion, a factor for eye color in the first chromosome, on purple, another eye color factor in the second chromosome (17). There are all kinds of gradations in the interaction of such factors. In our material presented above there is variety enough to overtax the descriptive words of Morgan of modifiers, disproportionate modifiers, differentiators, sensitizers, etc.

The dominance spoken of here in the discussion of duration of life factors therefore does not imply the usual meaning that goes with the classic terms dominant and recessive, as applied to contrasted pairs of allelomorphs.

It is a well known fact among geneticists, specially those working with *Drosophila*, that the designation of any mutant race, white eye for example, has reference only to that characteristic of it which is readily discernible. It is also regarded as a fact that the productivity and viability of such an individual is affected adversely as compared with the wild fly. Morgan(9)

goes a little farther and states that "The productivity of the individual (of any mutant)* is also much affected and the viability is lower than in the wild fly". While we do not subscribe entirely to that statement, inasmuch as our data show that there is at least one mutant which actually increases duration of life, it is apparently true in more cases than it is not true. Morgan continues: "It follows that whatever it is in the germplasm that produces white eyes, also produces other modifications as well, and modifies not only such 'superficial' things as color, but also such 'fundamental' things as productivity and viability". Such being the case, the name applied to the factor is only useful in designating the conglomerate of effects which behave as a single unit in inheritance, and we may perfectly well call the separate duration of life factors recognized in these experiments "Duration of Life factor 1, 2, 3, 4, and 5", each respectively associated with visible modifications black, purple, vestigial, arc, and speck. Logically such naming of these mutants is as sound and justifiable as to name them on the basis of morphological differences.

*The parenthetic expression is added to clarify the reference.

Summary and Conclusions.

This paper is the first attempt at localizing in the chromosomes the factors controlling duration of life. Five mutants in the second chromosome of *Drosophila melanogaster* were used as indices for five distinct factors that were recognized as having definite effects on duration of life. The five mutants were contained originally in one parent strain, which crossed with the wild stock, produced twenty-two distinct combinations. The behavior of these combinations with respect to duration of life was studied in a total of 24,287 flies.

It is shown that under constant environmental conditions, duration of life is controlled with extreme precision and exactness by genes present in the chromosomes. These same genes also control certain morphological characters. Through the biometric treatment of the data a better insight is obtained of the interactions of factors present in different parts of the chromosome affecting the same property of the individual, than has been possible with such characters as eye color and length of wing not susceptible to fine measurement.

It is also shown that some of the factors, although not sex linked, affect the sexes differently.

The above statements rest on the assumption that the units in the wild fly that are allelomorphs to the mutant genes control the same characters.

Literature Cited.

1. Pearl, R. and Parker, S. L. Experimental Studies on the Duration of Life.
I. Introductory Discussion of the Duration of Life in Drosophila.
American Naturalist, Vol. 55, pp. 481-509, 1921.
2. Id. II. Hereditary Differences in Duration of Life of Line-bred Strains
of Drosophila. Ibid. Vol. 56, pp. 174-197, 1922.
3. Id. III. The Effect of Successive Etherizations on the Duration of Life of
Drosophila. Ibid. Vol. 56, pp. 273-280, 1922.
4. Id. IV. Data on the Influence of Density of Population on Duration of
Life in Drosophila. Ibid. Vol. 56, pp. 312-321., 1922.
5. Id. V. On the Influence of Certain Environmental Factors on Duration of
Life in Drosophila. Ibid. Vol. 56, pp. 385-398, 1922.
6. Pearl, R. Id. VI. A Comparison of the Laws of Mortality in Drosophila
and in Man. Ibid. Vol. 56, 398-405, 1922.
7. Pearl, R. and Parker, S. L. On the Influence of Density of Population
upon the Rate of Reproduction in Drosophila. Proc. Nat. Acad. Sci. Vol.
8, 212-219, 1922.
8. Moenkhaus, W. J. The Effects of Inbreeding and Selection on the Fertility,
Vigor, and Sex-ratio of Drosophila ampelophila. Jour. Morph. Vol. 22,
pp. 123-154. 1911.
9. Hyde, R. R. Inheritance of the Length of Life in Drosophila ampelophila.
Indiana Acad. Sci. Rept. for 1913, pp. 113-123.
10. Loeb, J. and Northrop, J. W. Is there a Temperature Coefficient for the
Duration of Life? Proc. Nat. Acad. of Sci. Vol. 2, pp. 456-457, 1916.
11. Id. What Determines the Duration of Life in Metazoa? Ibid. Vol. 3,
pp. 382-386, 1917.
12. Id. On the Influence of Food and Temperature upon the Duration of Life.

- Jour. Biol. Chem. Vol. 32, pp. 103-121, 1917.
13. Northrop, J. H. The Effect of Prolongation of the Period of Growth on the Total Duration of Life. Ibid. Vol. 32, pp. 123-126, 1917.
14. Lutz, F. E. Experiments with Drosophila ampelophila Concerning Natural Selection. Bulletin Amer. Mus. Nat. Hist. Vol. 34, pp. 605-624, 1915.
15. Pearl, R. The Biology of Death. Philadelphia (Lippincott) 1922, 275pp.
16. Morgan, T. H. The Physical Basis of Heredity. Philadelphia (Lippincott) 1919, 305 pp.
17. Bridges, C. B. and Morgan, T. H. The Second Chromosome Group of Mutant Characters. In "Cont. to the Genetics of Drosophila melanogaster." Carnegie Inst. Publ. No. 278, pp. 123-304, 1919.
18. Bridges, C. B. Current Maps of the Location of the Mutant Genes of Drosophila melanogaster. Proc. Nat. Acad. Sci. Vol. 7, pp. 127-132, 1921.
19. Field, J. A. Some Advantages of the Logarithmic Scale in Statistical Diagrams. Jour. Pol. Econ., Vol. 25, pp. 805-841, 1917.
20. Lynch, C. J. An Analysis of Certain Cases of Intra-Specific Sterility. Genetics. Vol. 4, pp. 501-533.
21. Pearl, R., Parker, S. L., and Gonzalez, B. M. Experimental Studies on the Duration of Life. VII. The Mendelian Inheritance of Duration of Life. American Naturalist., Vol. 57, 1923 (In press).

Curriculum Vitae.

Bienvenido Maria Gonzalez was born March 22, 1893 in Apalit, Pampanga, Philippine Islands. He is the son of Dr. Joaquin Gonzalez and Florencia Sioco, and is eighth in a fraternity of ten males. He married Concepcion Rafols of Maasin, Leyte, P. I. on January 1, 1917, and had two sons Manuel (1917) and Gonzalo (1919).

He studied his first letters under his elder brothers and in private schools, and in 1902 passed his examinations to the academy "Colegio de San Juan de Letran" where he stayed until 1905. From 1905-1910 he attended public schools in the city of Manila. In 1910 he entered the College of Agriculture of the University of the Philippines, receiving the degree of Bachelor of Agriculture in 1913. He was appointed assistant in animal husbandry in the same institution in 1913, and in 1914 was awarded a fellowship for foreign study by the University of the Philippines. He attended the University of Wisconsin 1914-1916, taking general work in animal husbandry and specializing in animal genetics. He obtained the degree of Master of Science from that institution in 1915. He was appointed to the faculty of the University of the Philippines as instructor in animal husbandry (1916), assistant professor (1917), associate professor (1919), and professor (1920). He was elected by the alumni of the University of the Philippines as their first representative to the board of regents of their Alma Mater from 1918 to 1921. From 1921 to 1923 he was awarded a faculty fellowship by the U. of the Philippines to complete his education for the doctorate, and to specialize in animal genetics under Dr. Raymond Pearl of Johns Hopkins University. He attended the School of Hygiene, J. H. U. from May 1921 to date.

He is author of these papers:

1. The Changes Occurring in the Ripening Coconut, Phil. Agric. & Forest.
Vol. 3, pp. 25-31, 1914.
2. The Macapuno Coconut. Ibid. Vol. 3, pp. 31-32, 1914.
3. The Gestation of the Carabao. Jour. of Heredity. Vol. 10, pp. 374-375, 1919.
4. Foot and Mouth Disease at the College of Agriculture. Phil. Agric.
Vol. 8, pp. 77-78, 1919.
5. Practical Work in Animal Husbandry. Phil. Agric. Vol. 9, p. 33, 1920.
6. Range Cattle Management in the Philippines. Ibid. Vol. 9, pp. 59-65, 1920.
7. Hog Cholera in the College of Agriculture. Ibid. Vol. 10, 347-349, 1922.

A number of popular articles on animal husbandry topics in Manila dailies and weeklies.

